12 Rarity and evolution: some theoretical considerations

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12.1 INTRODUCTION

Does rarity matter in evolution? This question has no simple answer, because the terms 'rarity' and 'evolution' each denote complex rather than simple things. Evolution, in its broadest sense, incorporates all aspects of the origin and maintenance of biotic diversity by processes within and among species (e.g. selection and speciation). Rarity is likewise a compound concept, usually involving comparisons among populations or species (Gaston, 1994).

Gaston (1994) has proposed that the term 'rarity' be used in a relative sense to denote (say) the least abundant 25% of species in a community. This proposition has its merits, but other usages are also reasonable. For instance, rarity might indicate the subset of a rank-ordered list of species, starting with the least common, which collectively comprise 25% of total community abundance (this subset often includes a majority of species). Or, a species may be deemed 'rare' assessed against an absolute criterion, such as one of those that emerge from models of demographic stochasticity or Allee effects, or by its likelihood of being observed in a defined sample. For instance, a temperate-zone bird-watcher after a day of meagre birding in the Atacama Desert could reasonably conclude that all bird species there are 'rare'; with Gaston's definition, there are by convention exactly as many rare species there as anywhere else.

In this chapter, when considering a local community, the word 'rarity' will be shorthand for 'low population size'. When considering large biogeographical areas, 'rarity' may denote either a small total abundance for a species or a small range size (e.g. number of sites occupied), depending on context; 'spatial rarity' will be used to indicate the latter aspect of rarity.

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'Rarity' may be related to 'evolution' in many ways; a given component of rarity may be irrelevant to some aspects of evolution, yet critical for others (Ridley, 1993). The aim in this chapter is to provide an overview of our current understanding of how two aspects of 'rarity' – small local population size and small range size – influence evolutionary dynamics. The emphasis is on evolutionary theory, rather than empirical patterns (thus complementing other chapters in this volume, e.g. Chapters 10, 11) and particularly on unresolved or poorly explored conceptual issues. Although the consequences of rarity for microevolution are examined most closely here, some implications of rarity for macroevolution are also touched on.

To place current issues in a historical context, a capsule history of ideas about the role of population size in evolution is first presented. Next, we take a hierarchical approach to analysing the evolutionary implications of rarity. Some evolutionary implications of population size in a closed local community (i.e. where immigration is absent) are considered. After some comments on differences between ecological and genetical measures of population size, the influence of population size on neutral evolution, adaptive evolution, and sympatric speciation is discussed. The chapter then looks at the relation of population size to adaptive evolution in local communities open to immigration. Finally, it examines the more complex (but realistic) issue of species rarity at broader spatial scales, encompassing many local communities, where one must consider the effects of both total population size and range size on evolution.

One message of this chapter is that rarity may have differing evolutionary roles at different spatial, temporal and comparative scales of analysis. Many different kinds of comparisons are possible. One could compare evolution of two species (one common, the other rare) at the same site; or of pairs of populations at different sites within the same species' range; or of species as a whole over their entire ranges; or of all rare species vs. all common species (or all rare populations of a species vs. all common populations). A second message that runs through the chapter is the importance of grounding evolutionary questions in a firm understanding of population dynamics.

12.1.1 Historical context

Ideas about the role of rarity in evolution have long been central to conceptual controversies in evolutionary biology. Charles Darwin (1859 [1964: 53; see also 105, 107]) argued that large and widely distributed populations are the locus of most significant evolution:

> It is the most flourishing . . . , the most dominant species – those which range widely over the world, are the most diffused in their own country, and are the most numerous in individuals, – which oftenest produce well-marked varieties, or . . . incipient species.

As summarized crisply by Leigh (1986: 192–193), Ronald Fisher likewise believed that:

> large populations allow more mutation, discriminate selective advantages more precisely, and retain a larger proportion of favourable mutations, than do smaller ones. In practice, large populations vary most. Thus, one expects a smaller number of large populations to be increasing at the expense of a larger number of small ones. Accordingly, the study of evolution should focus on abundant species, which are the fount of adaptation.

This is Darwin's worldview, dressed up in modern genetics.

Many evolutionists have argued against the evolutionary centrality of large populations. Wright's shifting balance theory (Wright, 1931, 1977) highlighted a potential creative role for drift, permitting small populations to move between adaptive peaks. The disagreement between Fisher and Wright on the role of population size is one of the oldest controversies in population genetics (Maynard Smith, 1983a) and arises from sharply different views of epistasis (Wade, 1992).

The shifting balance theory (Eldredge, 1985) led many evolutionists to claim that major adaptive evolution is less likely in large populations. Mayr (1982: 604), for instance, asserts that 'large, widespread populations – in fact all more populous species – are evolutionarily inert'. The assumption that rarity promotes evolution has figured prominently in the debate over 'stasis' in the fossil record (e.g. Eldredge and Gould, 1988; Stanley, 1990).

Other evolutionists (e.g. Maynard Smith, 1983b) doubt that large population size hampers evolution: 'The supposed evolutionary inertness of large populations . . . is based on no evidence' (Coyne, 1994). Stasis, for instance, may reflect stabilizing selection (Charlesworth *et al.*, 1982). Theoretical studies of the interplay of drift, selection and gene flow qualitatively agree with Darwin and Fisher: adaptive evolution should often be more rapid and precise in larger populations (Holt, 1987).

Analysis of the shifting balance theory is a highly active area of theory (e.g. Barton and Rouhani, 1992). The jury is still out on the importance of this process (Crow *et al.*, 1990; Wade, 1992). 'Punctuational' changes need not imply an important role for rarity: peak shifts may occur in large populations, given transient environmental changes or increased genetic variance (Kirkpatrick, 1982; Merrell, 1994).

Ernst Mayr's theory of peripheral speciation emphasizes episodes of very low abundance in isolated populations (e.g. 'founder effects': Provine, 1989; Barton, 1989). By contrast, the standard Darwinian view is that speciation emerges as a byproduct of adaptive evolution proceeding independently in isolated populations. Maynard Smith (1989: 280) observes that even if small peripheral populations do exhibit more rapid speciation, this may not be because of their population size. If, within a species, populations at low density more often experience strong directional

selection than do more abundant populations and peripheral populations tend to be isolated from gene flow, small peripheral populations may incidentally experience factors that jointly facilitate speciation, irrespective of their rarity. Local rarity may thus be correlated with speciation, but not causally relevant.

To conclude this historical sketch, it is clear that evolutionists differ sharply in their views on the role of rarity (in its meaning of 'low population size') in evolution. The lack of unanimity on such a fundamental aspect of the history of life is rather astonishing.

12.2 EVOLUTION IN LOCALLY RARE POPULATIONS

12.2.1 Closed communities

To clarify the interplay of rarity and evolution, it is helpful to begin with the simplest case, namely a closed community which after its initial establishment is closed to further immigration or colonization. In a local community, a species is 'rare' if it has low population size, relative to other species in the community. Rarity may influence many aspects of evolution in a closed community, from 'arms races' in specialist predator–prey interactions (Schaffer and Rosenzweig, 1978) to long-term responses to environmental change (Holt, 1990).

(a) A methodological difficulty

A significant gap in relating evolutionary theory to field data is that the relevant population size is not census abundance, N_{cens}, but 'effective population size', N_e, which governs both drift and the amount of variation available for selection (Hedrick, 1983; Crawford, 1984; Holt, 1987). Even in apparently thriving populations, N_e may often be low enough for significant drift (for examples, see Lande, 1979; Husband and Barrett, 1992).

Temporal fluctuations in abundance imply $N_e < N_{cens}$ (Hedrick, 1983; Begon, 1992). N_e is approximately the time-averaged harmonic mean of population size (Crawford, 1984), a quantity heavily biased toward low N. For example, a population that spends a fraction q of generations at N_{low}, and the remainder at huge numbers, has $N_e < N_{low}/q$ (Holt, 1987). A typically abundant species with occasional excursions to low densities may have a lower N_e than a rare species with stable dynamics. Crawford (1984) reports one to two order-of-magnitude differences between census and effective population sizes in arthropods, but smaller (two-fold) differences in large vertebrates (possibly reflecting differences in the scale of population fluctuations in these two groups).

Variation maintained in a mutation-drift balance increases with N_e (Hedrick, 1983), as does genetic variance of neutral quantitative characters

(Lynch, 1994). Common species indeed often harbour more neutral genetic variation than rare species (Chapter 10; Nei and Grauer, 1984). For instance, Hamrick *et al.* (1991) compared allozyme diversities of common and uncommon tree species on Barro Colorado Island, Panama, and found locally rarer species had lower genetic diversity.

The relevant time-series that determines N_e may be very long. Gillespie (1991: 54) notes that though species with population sizes in the range $10–10^3$ exhibit unusually low levels of heterozygosity and a positive correlation between population size and heterozygosity, for species exceeding 10^4 in population size heterozygosity is essentially independent of N. This could be a genetic signature of population fluctuations over long time-scales. Nei and Grauer (1984; see also Barrett and Kohn, 1991) argue that contemporaneous interspecific patterns of protein heterozygosity reflect Pleistocene bottlenecks. (By contrast, sensitivity to infrequent bottlenecks may not characterize quantitative traits, which have relatively high mutation rates: Lande, 1980.)

Pimm (1991) has observed that variance in abundance seems to increase, the longer one observes a population. Short-term studies are likely to overestimate N_e. There seem to have been no attempts to compare relative rankings of species in a community by N_{cens} and by N_e. Were the two rankings similar, this would suggest consistency in current rank-order abundances over evolutionarily significant time-scales.

Given that a local population persists, its abundance must be bounded away from zero. Populations with low average abundances should tend to have low temporal variance in abundance; populations with high average abundances can persist in the face of higher variance. This dynamical constraint suggests that populations may differ less in N_e than in average N_{cens}; this is because N_e is determined principally by population lows (and persisting populations cannot get too low in abundance and still persist), whereas average abundance is strongly influenced by population highs (which can vary widely without affecting the likelihood of persistence). It would be a useful theoretical exercise to assess systematically the effect of different patterns of population dynamics on N_e. In any case, gauging the relevance of local rarity to evolution requires consideration of the dynamical behaviour of populations – not just mean abundances.

(b) Rarity and rates of neutral evolution

Neutral evolution may matter on its own (e.g. in molecular evolution: Nei, 1987) or as a null model for phenotypic evolution (Lynch, 1994). A simple, striking prediction of the theory of neutral molecular evolution is that the rate of allelic substitution at a single locus is the per capita mutation rate, independent of N_e (Kimura, 1983). Unless the mutation rate varies with N_e, there should be no correlation across species between population size and the average rate of neutral evolution. Models of neutral phenotypic

evolution likewise predict that expected between-population variance in mean genotypic values increases linearly with time (Lynch, 1994), independent of N_e.

Population size does not influence the rate of neutral evolution within a lineage. Does this imply rarity is irrelevant to neutral evolution in a local community? Not at all! In comparing a rare species with a common one, on average they should not differ in evolutionary rates. However, if at the level of the entire community we compare evolution in rare species (as a class) with common species (as a class) we must account for differences in species richness. In communities, different abundance classes typically differ in species richness.

Interspecific variation in abundance typically fits lognormal or logseries distributions (May, 1975; Tokeshi, 1993), which are right-skewed, with more moderately rare species than common species. Because mutation and drift are stochastic, species will vary in their realized rates of evolution. If an evolutionary 'novelty' is defined as a phenotypic change greater than a specified amount (compared with a species' ancestral condition), one is more likely to observe a novelty first arising in moderately rare species than in common species, simply because there are more of the former, providing a larger sample for the stochastic evolutionary process. Arnold and Fristrup (1982) make a similar point about the evolutionary scope of clades differing in species richness.

So, given neutral evolution, there may be emergent macroevolutionary effects of population size at the community level, even if population size has no average effect on the rate of microevolution in any species. The utility of this insight rests on the largely untested potential for neutral models to explain interesting patterns of phenotypic evolution. In most cases, phenotypic evolution is obviously driven by selection.

(c) Local rarity and adaptive evolution: direct effects

Rarity can directly affect adaptive evolution if the rank-order fitness of phenotypes or genotypes varies with population size. From the perspective of an individual organism, population abundance is one of many environmental factors that may influence its fitness (Chapter 9). There are two basic ways this can happen, encapsulated in the distinction between 'hard' and 'soft' selection (Hedrick, 1983). Standard models of density-dependent selection (e.g. Begon, 1992; Charlesworth, 1994) analyse selection at those life stages which determine abundance. The outcome of selection in these models is to increase carrying capacity ('hard' selection). Rare populations which experience hard selection and persist should, as a byproduct, become less rare (Gomulkiewicz and Holt, 1995).

But rank-order fitness can vary with population size, without reciprocal effects of selection on population size ('soft' selection). Orians (Chapter 11) argues that the reproductive syndromes of rare plants may differ

systematically from common plants (e.g. in being less dependent on specialist pollinators; see also Kunin and Gaston, 1993). Such adaptive consequences of rarity need not make populations more abundant as a byproduct of selection.

The literature of evolutionary ecology is replete with verbal arguments and formal theoretical models exploring coevolutionary consequences of population size (e.g. Rosenzweig *et al.*, 1987; Begon, 1992). Two examples suffice to illustrate these ideas:

- Populations rare because of interspecific competition may evolve enhanced interspecific competitive ability, whereas competitive dominants may be selected for improved intraspecific competitive ability (Pimentel *et al.*, 1965; Aarssen, 1983).
- If predators consume substitutable prey, selection on attack rates should be biased toward abundant prey types (Holt, 1977).

Such effects are doubtless important. However, within a community, rare species are a highly heterogeneous lot. Local rarity has myriad causes (Gaston, 1994); many distinct evolutionary syndromes can thus be associated with rarity. It is unlikely anything very sensible can be said about the adaptive importance of rarity, *per se*, outside carefully delimited comparative contexts (e.g. between sympatric congeners, as in Orians' example in Chapter 11).

Such comparisons often benefit from being cast within an explicit or implicit model for population dynamics. Let us assume each species in a local community follows a generalized logistic growth model:

$$\frac{dN_i}{dt} = [r_i - d_i N_i - m_i(t)]N_i$$

where N_i is the local abundance of species i, r_i its intrinsic rate of increase, d_i is the strength of density-dependence species i exerts on itself, and $m_i(t)$ is temporally varying density-independent mortality imposed on species i (e.g. from episodic disturbances). Species i deterministically persists if:

$$r_i - \langle m \rangle_i > 0$$

where $\langle m \rangle_i$ is the time-averaged mortality experienced by species i. The time-averaged abundance of population size (Levins, 1979) is:

$$N^*_i = (r_i - \langle m \rangle_i)/d_i.$$

A species may be rare in a closed community because of low r_i (e.g. the habitat is near the edge of its fundamental niche), or because density dependence is strong (high d_i), or because of frequent, severe disturbances (high $\langle m \rangle_i$). These very different dynamical reasons for rarity could imply quite distinct selective regimes.

Yet the relation between the ecological environment which determines population dynamics and the selective environment which generates

evolutionary dynamics is complex and can at times be counter-intuitive. Ecologists often casually assume that as a given factor becomes more important in limiting or regulating population size, that factor automatically becomes more important in selection. The folk wisdom is that 'evolution works hardest where the shoe pinches worst' (W. Kunin, personal communication). For a spatially homogeneous system, the consumer-resource model (MacArthur, 1972) can be used to illustrate two distinct classes of counter-example to this intuition.

Let C_i be the density of consumer species i, and R_i the availability of its required resource. We assume each consumer species exploits its own exclusive resource (i.e. no interspecific competition among consumers) and grows according to:

$$dC_i/dt = C_i\,(a_i b_i R_i - m_i)$$

where a_i is the per unit rate of uptake, b_i converts consumption into consumer births and m_i measures density-independent mortality. Assume resource dynamics are given by:

$$dR_i/dt = I_i - u_i R_i - a_i R_i C_i$$

where I_i measures resource input, and u_i the rate of loss other than to consumption. At equilibrium, resource and consumer abundances are, respectively:

$$R_i^* = m_i/a_i b_i$$

and:

$$C_i^* = b_i I_i/m_i - u_i/a_i$$

In a local community, as noted above, one consumer population may be rarer than another for any of a number of distinct dynamical reasons. In this resource–consumer system, a consumer may be rare because it experiences a high mortality rate (high m_i), or is ineffective at acquiring the resource (low a_i), or has a low-quality resource (low b_i). Alternatively, a consumer population may be rare because its resource has a low input rate (low I_i) or a high loss rate (high u_i). The former class of reasons focuses on parameters which enter directly into the consumer's own growth equation. By contrast, the latter class of reasons for rarity involve parameters of the resource, not parameters of the consumer population. Only the former parameters are directly accessible to selection in the consumer.

Now assume that consumers vary intraspecifically in exploitative ability, and that such variation affects only the attack rate a_i. For a moment, assume that the consumer does not influence resource availability. The strength of selection for an increase in attack rate is given by:

$$d/da_i\,[(1/C_i)dC_i/dt] = b_i R_i.$$

The greater the R_i, the greater is the strength of selection for increasing the rate of exploitation on the resource. Conversely, decreased resource

availability reduces the strength of selection for improved exploitative abilities (Abrams, 1986, elaborates this theme). As food becomes more important in limiting population growth (i.e. lower R_i), the strength of selection for improved food acquisition can become weaker, not stronger.

If we assume that there is a trade-off between the ability to acquire the resource and ability to withstand mortality factors, this may imply the existence of an optimal attack rate. Formally, let:

$$M_i = M + m'_i(a_i)$$

where M is fixed mortality and $m'_i(a_i)$ is the additional mortality that accrues because of resource consumption. Assume $dm'_i/da_i > 0$ and $d^2m'_i/da_i^2 > 0$ (e.g. more intense foraging has risks which increase at a faster than linear rate). The optimal phenotype is found from:

$$d/da_i\,[(I/C_i)dC_i/dt] = 0$$

or:

$$b_iR_i = dm'_i/da_i.$$

The lower the R_i, the lower is the optimal uptake rate (and the death rate). In a resource-poor environment, consumers may evolve toward lower exploitation rates.

Now assume that the resource–consumer interaction is in demographic equilibrium, so consumption limits resource availability. After setting $R_i = R_i^*$, the optimal uptake rate is found from:

$$m_i/a_i = dm'_i/da_i,$$

an expression which is independent of the parameters I_i, u_i and b_i. Differences between species in these parameters affect local consumer abundance but do not influence the optimal consumer phenotype. Moreover, an increase in fixed mortality (M) increases R_i^*, which indirectly increases the optimal rate of resource exploitation, even at the expense of greater net mortality (m_i).

The above model illustrates several general points. First, population size can be influenced by many factors not part of the selective environment directly experienced by individuals. In a local community, one species may be rare and another common (e.g. because of differences in the renewal rates of required resources), without any necessary qualitative difference in the selective environments experienced by individuals.

Second, increasing the magnitude of a limiting factor need not automatically evoke a selective response that tends to counter that environmental change (given the existence of genetic variation). Elsewhere (Holt, 1996a,b, and see below) it has been similarly shown that in populations with a source-sink structure, as a population becomes increasingly restricted to the source the strength of selection favouring

adaptive evolution in the sink becomes weaker, not stronger. A fundamental problem in understanding the evolutionary implications of local rarity is thus articulating the relation between factors influencing local population size, and those influencing adaptive evolution. The above model and the results reported in Holt (1996b) illustrate that this relation may be subtle, non-obvious and often counter-intuitive.

Third, the particular conclusions reached above clearly apply to a particular model. Change the assumptions of the model, and the resulting predictions are likely to change. The aim in this chapter is not to champion the specific conclusions of this model, but rather to suggest that discussions of the relation of rarity to evolution need to be cast in the context of explicit population dynamic models, and that intuitive notions about the mapping of limiting factors on to selective factors may at times be off-base.

(d) Local rarity and adaptive evolution: indirect effects

Population size indirectly influences adaptive evolution via control of the supply of heritable variation, and by altering the relative importance of selection and drift. Theory predicts that large populations generate more novel mutations per generation and retain more variation against the influence of drift (Holt, 1987). Sometimes this is unimportant. For instance, in constant environments, if relative fitnesses can be described by a function with a single optimum, even weak selection can maintain populations near their optimal phenotype, except in quite small populations (Lande, 1980).

Wright's shifting balance theory suggests that small (but not too small) populations may have the greatest capacity for adaptive evolution. However, this theory works best when considering conspecific populations with the same adaptive surface. In the absence of a universal metric for describing adaptation across species in a community (which seems improbable *a priori*) it may be difficult to attach much meaning to the claim that rare species are more, or less, precisely adapted than are common species.

The metaphor of adaptive landscapes may not be very useful for natural enemy–victim interactions, which typically involve frequency-dependent selection. Seger (1992) argues that natural enemy–victim systems are prone to evolutionary instability. Cyclic or chaotic dynamics in gene frequencies can force some allelic frequencies to drop to low values, fostering the loss of variation in small populations. Long-term evolutionary instability in enemy–victim systems (if it occurs at all: Rosenzweig *et al.*, 1987) requires both species to maintain variation, so should be most likely if both species sustain large effective population sizes.

One indirect evolutionary effect of rarity which has been recently recognized is that small populations tend to harbour larger loads of deleterious mutations than do large populations, and so may be more

prone to extinction via 'mutational meltdown' (Lynch and Gabriel, 1990; Lande, 1994). This maladaptive evolutionary process can lead to the eventual disappearance from a local community of species which were initially adapted to local conditions, leading to differential extinctions of rare species far beyond the expectations of demographic stochasticity alone (Lande, 1994).

(e) Local rarity in temporally varying environments

Environmental change can induce phases of directional selection as populations move towards new phenotypic optima (Grant and Grant, 1989). Directional selection experiments show that both initial rates of response to selection and ultimate selection limits increase with population size, qualitatively matching theory (Hill and Caballero, 1992). As noted above, temporal variation in abundance depresses N_e. This enhances drift, on the one hand making shifting balance evolution more likely, but on the other depleting the pool of variation. Population fluctuations may also lead to temporal variation in selection, which in turn can make peak shifts more likely without drift (Kirkpatrick, 1982; Merrell, 1994). The overall effect of transient phases of local rarity on adaptive evolution, taking into account all these factors, is not at all clear.

Recently, theoreticians have explored evolutionary dynamics of populations in changing environments (e.g. Holt, 1990; Lynch and Lande, 1993; Gomulkiewicz and Holt, 1995). In a closed community, evolution is the only feasible route to survival given sufficiently great environmental change. Rare species may be especially vulnerable to extinction in changing environments. Low N_e implies low variation, reducing the rate of response to selection in a novel environment. There is a roughly log-linear increase in the permissible rate of environmental change – beyond which extinction is inevitable – with increasing N_e (Lynch and Lande, 1993).

After severe environmental change, species should decline in number even as they adapt. Given a rare and a common species with the same genetic variation, the rare species is more likely to dip to densities where extinction is likely due to demographic stochasticity (Gomulkiewicz and Holt, 1995). Though large populations are no buffer against large environmental change, even small changes can potentially endanger rare populations – including those with the genetic wherewithal to adapt to changed circumstances.

These conclusions concern pairwise comparisons of common and rare species. Interspecific phenotypic variation usually greatly exceeds intraspecific variation. In a closed local community, the only species likely to survive a radical environmental change may be rare species – simply because a greater initial range of phenotypes was available among rare species, increasing the likelihood that at least one species was preadapted to the change. Environmental change often leads to dramatic shifts in

dominance, with initially rare species becoming abundant (Holt, 1995). Long-term community evolution may be dominated by the descendents of species which were rare at the time of large environmental change, merely because this class of species is relatively speciose.

(f) Rarity and sympatric speciation

Macroevolution in a closed community is likely to be largely driven by differential species extinction, which should be biased toward rarer community members. The only other macroevolutionary process which can operate in a closed community is sympatric speciation.

The most widely accepted mechanism for sympatric speciation is polyploid speciation. Hybridization between sexual species produces allopolyploids, a process that occurs reasonably often in plants (Grant, 1981). Considering all potential parental pairs of species, the rate of hybridization should be low for pairs of rare species, versus pairs with at least one common species. Indeed, in many plant-pollinator systems, rare species may be particularly vulnerable to hybridization with commoner species (W. Kunin, personal communication). This can lead to extinction, but also provides a source for polyploid speciation. There seems to be no formal theory bearing on this potential effect of population size on rates of allopolyploidy.

Autopolyploids are created by meiotic irregularities creating diploid gametes, which then combine. The rate of production of meiotic anomalies is likely to be proportional to population size. All else being equal, common species will be the most likely progenitors of autopolyploid species (Rosenzweig, 1995).

Other mechanisms for sympatric speciation are more controversial and depend upon density-dependent competition and heterogeneous habitats or resources (e.g. Rosenzweig, 1995; Wilson, 1989). Population size is not well correlated with local niche breadth (a measure of heterogeneity in habitat or resource use: Gaston, 1994), so there is no obvious reason to expect local rarity to affect the likelihood of these modes of sympatric speciation.

12.2.2 Open communities

Now consider a local community open to immigration, but without reciprocal ecological or evolutionary effects on the source pool for immigrants. Communities on oceanic islands often match this scenario reasonably well. Spatial openness in a local community has both intraspecific and interspecific effects. First, immigration into established populations permits gene flow to interact with selection, mutation and drift. Second, local species richness can be enhanced. Species may occur which could not persist in a closed community, either because they are

vagrants (Gaston, 1994) or sink populations (Pulliam, 1988; Holt, 1993); or because they can re-colonize following local extinction; or because spatial openness permits ways of life impossible in closed communities, increasing the 'effective niche space' of the community (Holt, 1993).

Suggestive evidence of the evolutionary importance of rarity in open communities comes from analyses of island biotas. Diamond (1984, Figure 17) reported that endemism of Pacific island birds (at the species level or higher) increases with both island area and distance from continental sources. The following paragraphs build on Diamond's explanations for this pattern to identify several distinct evolutionary influences of rarity, possibly revealed in these area and distance effects in endemism.

Assume that, in the source, species have fixed properties. All colonization is from source to island. For species i, let c_i (A,d) be its colonization rate on to islands of given area A and distance d from the source, and e_i (A,d) its local extinction rate. In general (MacArthur and Wilson, 1967) colonization increases with area and decreases with distance; extinction decreases with area (a proxy for population size) and increases with distance. The fraction of islands in a given area–distance class with species i is p_i – the 'occupancy' of islands by species i (Hanski, 1991). Occupancy changes by:

$$\frac{dp_i}{dt} = c_i\,(1 - \mathrm{p_i}) - e_i p_i \qquad (12.1)$$

At equilibrium:

$$p_i^* = c_i/(c_i + e_i).$$

(a) Area effects on endemism

Populations on different islands of the same size and area are likely to differ in age (i.e. time since colonization). With constant extinction rates, at equilibrium all those populations within a given island area–distance class should exhibit an exponential distribution of ages. Assume that an evolutionary 'clock' starts ticking at colonization. If after T time units, divergence is sufficient to be deemed systematically relevant, a fraction $exp[-e_iT]$ of island populations should have survived long enough to become systematically distinct.

Among populations on different islands stemming from a given ancestral source species, those on larger islands should be observed to be more differentiated, for two reasons related to population size. First, they tend to be older (because they are larger in local abundance and so have lower extinction rates), and thus will have had more opportunity to become evolutionarily distinct (Diamond, 1984). Second, complementing this ecological effect, for the genetical reasons sketched above, larger populations may also adapt more rapidly to fixed or changing environments.

Immigration may also contribute to area effects on endemism. The number of immigrants per species per unit time into an island should scale with a linear dimension of island size (MacArthur and Wilson, 1967), while the resident population size should scale with this linear dimension squared. The relative contribution of immigrants to an island gene pool should thus decline with increasing island area, for islands equidistant from the source.

This will not affect neutral evolution; a very small amount of gene flow prevents neutral genetic differentiation, almost independent of population size (Hedrick, 1983). By contrast, gene flow may be more likely to constrain **adaptive** evolution in locally rare than in locally common populations, relative to a source population (e.g. Antonovics, 1976; Endler, 1977; Holt, 1987). Consider a population with discrete generations and viability selection at a diploid locus. $N(t)$ is the local population size at the start of generation t, $N'(t)$ population size following selection, and $i(t)$ the number of immigrants. Assume that immigrants are fixed for allele 2, and allele 1 is locally favoured. Let w_{ij} be the fitness of genotype ij; and assume both w_{11} and $w_{12} > w_{22}$. Over T generations, allele 1 increases when rare if:

$$\prod_{t=0}^{t=T-1} L(t) > (w_{22}/w_{12})^T$$

where $L(t) = N'(t)/[N'(t) + i(t)]$ is the fraction of breeding adults recruited locally, rather than by immigration (Nagylaki, 1979; Holt, 1987).

With constant abundances and immigration rates, persistence of the locally favoured allele requires $w_{12} > w_{22}\ (1 + i/N')$. Alleles with small positive effects on fitness are more likely to be retained if population size is large, relative to immigration. Given islands of area A, immigration scales as $A^{1/2}$ and population size as A; the selective advantage needed for retention of a locally favoured allele thus scales with $(1 + A^{-1/2})$. This implies that for a fixed immigration rate, rare (small island) populations are more vulnerable to gene flow. Moreover, if local population size fluctuates, the swamping effects of gene flow are magnified (Holt, 1987). The effect of demographic stochasticity looms larger in small populations, leading to fluctuations that further aggravate the effects of gene flow.

(b) Distance effects on endemism

The distance effect on endemism could reflect both within- and between-species consequences of rarity. Immigration increases population longevity (Brown and Kodric-Brown, 1977; Holt, 1993, and above), possibly increasing the scope for local evolution. However, as Diamond (1984) notes, such immigration also hampers local differentiation due to gene flow. The observed distance effect on endemism may imply that the genetic

effect of gene flow (hampering differentiation) outweighs its ecological effect (enhancing local population persistence). In the above model, $i(t)$ decreases with distance; distant islands should be less subject to gene flow, permitting greater differentiation.

This within-species effect of distance on differentiation overlays a complementary between-species effect. Species vary greatly in extinction rates (often paralleling differences in local N). The species turnover predicted by island biogeography on close inspection reveals the churning of rare species (Williamson, 1981; Schoener and Spiller, 1987). Gaston (1994) suggests that many rare species in open communities may be 'vagrants', unable to persist without immigration and presumably prone to high extinction rates.

It is easy to show, using an elaboration of (12.1), that given heterogeneous extinction rates, as one decreases overall colonization rates, island communities become biased towards species with low extinction rates, with a corresponding opportunity for more evolution. Averaged across species in a community, the mean longevity of island populations should increase with island distance. This interspecific effect compounds the intraspecific effect of a weakening of gene flow with distance, leading to the observed pattern of greater endemism on more distant islands.

(c) Local rarity as an indicator of evolutionary 'traps' in open communities

As noted above, many rare species in open communities may be vagrants. Why don't vagrant populations maintained by immigration evolve by natural selection so as to become responsible populations, self-sustaining in the local setting?

A 'vagrant' population that persists by immigration is a sink population (Pulliam, 1988; Holt, 1993). Theoretical models (Holt and Gaines, 1992; Holt and Gomulkiewicz, in press) suggest that the lack of adaptive evolution in sink populations may not be because gene flow hampers local selection, but instead simply reflects the fact that the vagrants are maladapted to the local environment in the first place. This can be seen using the above criterion for selection in the face of gene flow. Assume that at the start of generation t there are $N(t)$ individuals, all homozygous for allele 2, with absolute fitness in the local environment w_{22}. The population declines geometrically; after reproduction there are $N'(t) = N(t)w_{22}$ individuals. An aliquot of I individuals homozygous for allele 2 immigrates; after censusing there are $N(t+1) = N'(t) + I$ individuals. The equilibrial population size is $N = I/(1 - w_{22})$.

Now, introduce a very small number of individuals with allele 1 in heterozygous form. After substitution for N in the above criterion for a locally favoured allele to increase when rare, we find that in a sink population maintained by immigration the locally favoured allele 1

increases when rare if and only if $w_{12} > 1$. Note that this criterion for selection to enhance local adaptation is independent of the rate of immigration. Let $dw = w_{12} - w_{22}$ denote the effect of allele 1 upon individual fitness in the heterozygote. For $w_{22} < 1$, if dw is sufficiently small, $w_{12} < 1$. Hence, alleles of small positive effect on fitness cannot be favoured in a sink habitat. The evolution of adaptation by natural selection in a sink may require the availability of mutations of large effect (Holt and Gomulkewiecz, in press). If all available mutations have small effects on fitness, a sink habitat could remain a sink over extended time-scales, with no local adaptation.

Rare populations maintained by immigration may be observed not to adapt to the local environment, not quite because gene flow hampers local adaptation, but because rarity itself is a signature of low immigrant fitness. In this model, the influence of population size on the magnitude of gene flow disappears as a causal explanation for the lack of local adaptation in a rare sink population, once one properly accounts for the demographic as well as genetic effects of immigration (Holt and Gomulkiewicz, in press).

Hence, in an open community, rare species may be both less differentiated (from source populations) and less well adapted to the local environment, for several distinct reasons:

- In a community at equilibrium between colonization and extinction, rare species are more prone to extinction, and so on average are younger (the expected correlation between rarity and age may break down in non-equilibrial communities).
- If rare species persist, they are more vulnerable to gene flow (for a given rate of immigration).

In the latter case, local rarity is directly implicated in the lack of differentiation or adaptation. However, some species (vagrant populations in sink habitats) may be rare because they are maladapted and sustained by immigration; in this case, rarity is merely correlated with a lack of differentiation or adaptation, and is not its cause.

12.3 EVOLUTIONARY EFFECTS OF SPATIAL RARITY

Having examined in detail the evolutionary implications of rarity in first closed, then open, local communities, the next logical step is to move up in spatial scale to consider evolutionary effects of rarity for species distributed among several to many local communities. Entirely new evolutionary processes arise at larger spatial scales (e.g., group selection, allopatric speciation). The burgeoning literature on the evolutionary effects of population structure and metapopulation dynamics (e.g. Olivieri *et al.*,

1990; McCauley, 1993; Hastings and Harrison, 1994; Whitlock, ms.) will not be synthesized here; instead, let us highlight some general issues worthy of further attention.

Among species with comparable dispersal abilities, widespread species by definition have more local populations than do spatially rare species. For simplicity, consider species occupying discrete habitat patches, each patch potentially harbouring a population. We can describe a species' range with a population–abundance distribution, $p(n)$ (where local population size = n), which is a function giving the number of local populations falling into each abundance class. The total number of patches occupied is $p_T = \Sigma\ p(n)$ (a measure of patch occupancy) and total population size is $N_T = \Sigma np(n)$ (both summations are over n). Average local abundance is N_T/p_T.

Different populations coupled by dispersal comprise a metapopulation (Hanski, 1991). A rare species, in a geographical sense, has a small metapopulation ('spatial rarity'). In practice, the entire range of a species can rarely be usefully viewed as a single metapopulation, because of disjunct ranges and the sheer effects of isolation by distance in very large ranges (Maurer and Nott, in press).

As noted in the Introduction, when examining species over broad geographical areas there are several distinct facets of rarity, including total population size, N_T, and the number of local populations, p_T. As with local rarity, different dynamical reasons for spatial rarity may have different evolutionary consequences. One factor which arises in comparing spatially rare versus widespread species is that the latter may exhibit spatial heterogeneity in abundance and/or selective environments, which can have important implications for species-wide evolution.

For a fixed mean local abundance, N_T decreases linearly with decreasing p_T. A positive correlation between local abundance and range size (Brown, 1984; Lawton, 1993; Gaston, 1994) implies that spatially rare species have disproportionately low N_T, compared with this expectation. For neutral evolution, the evolutionarily relevant population size for species with stable dynamics is essentially N_T (Nei, 1987). Likewise, if the selective environment is spatially homogeneous with a single adaptive peak, the population size governing the input of potentially useful adaptive variation is ultimately the entire species' population. Our earlier conclusions about the effect (or lack thereof) of local population size on local evolution carry over wholesale to the effects of total population size on evolution at the level of entire species. This is basically Fisher's view (Wade, 1992).

As with local abundance, current range sizes may not accurately measure effective N_T. For instance, a species that experiences a sharp reduction in range, say because of climate change, may have a long transitional phase with considerably more genetic variation than expected from equilibrial genetic models.

As with local rarity, a species may be rare in a geographical sense for

many different dynamical reasons. For instance, in a 'classical' metapopulation (Hanski, 1991), the incidence of a species in a landscape is determined by a balance between colonization and extinction rates. Two species could be equally rare, one because of low colonization rates, the other because of high local extinction rates. They should evolve differently, despite their comparable range sizes; the species with frequent local extinction has little scope for evolution to hone local adaptations, compared with the species with low colonization rates.

One limiting case of spatiotemporal dynamics is to imagine that after speciation an initial bout of colonization spreads species over a landscape, with only minor subsequent dispersal among established populations (relative to local population sizes). Gene flow will not constrain local adaptation, but can still enrich local variation. The principal difference between spatially rare and widespread species will be in the number of populations making them up, scaling the pool of available variation, and defining the potential for a shifting balance process to operate.

There are hints in evolutionary theory that the size of a metapopulation (= number of local populations) may be important, independent of its effects on N_T. In the shifting balance process, any single population has a low probability of peak transition. The species-wide probability of a transition increases with p_T (Maynard Smith, 1983a; Newman *et al.*, 1985; Holt, 1987; S. Wright, as reported in Moore and Tonsor, 1994). Hence, species with wide ranges (numerous demes, i.e. large p_T) might evolve more readily by a shifting balance mechanism than species with narrow ranges.

But there is a fundamental difference between the size of a local population and the size of a metapopulation (p_T). All individuals in a local population, to a reasonable approximation, experience the same environment. The different 'individuals' (= demes) of metapopulations necessarily occur in different places. The larger a metapopulation, the larger the area it encompasses. A basic fact about the earth's surface is that physical and biotic heterogeneity scale with area (Williamson, 1981). Such spatial heterogeneity within a species' range has several consequences:

- If it translates into spatial variation in the selective regime, different populations will have different local selective optima. This permits adaptive spatial differentiation, but vitiates the range size effect on the likelihood of a shifting balance process across an entire species, because different populations will be under the influence of different adaptive peaks. The literature on shifting balance has largely ignored spatial heterogeneity.
- There may be considerable variation in local abundance within species' ranges, a pattern which Lawton (1994) refers to as the spatial 'texture' of abundance. This may not affect evolution if the selective environment is spatially uniform. However, the details of range texture – and its

underlying dynamical causes – matter a great deal if selection varies spatially. With dispersal and interbreeding, selection within a species involves an averaging over space. The way this plays out is critically influenced by how the selective environment and local abundance covary.

For instance, Endler (1977) argued that gene flow did not prevent local selection from producing clinal variation. This conclusion was based on models in which populations at adjacent points along an environmental gradient had roughly equal abundances, leading to reciprocal effects of gene flow which cancelled out. By contrast, gene flow between populations varying in abundance may be highly asymmetrical. High rates of immigration into rare populations can prevent local adaptation (see above). If the spatial texture of abundance includes a great deal of local variation in abundance, rare populations will typically neighbour abundant populations, leading to potential high rates of gene flow into rare populations. By contrast, if abundances change gently along smooth environmental gradients, rare populations will mainly have other rare populations nearby; the rate of immigration may tend to scale proportionally with local carrying capacity. Thus, gene flow should have the greatest homogenizing effect if there is substantial yet spatially uncorrelated spatial variability in abundance.

If spatial variation in abundance and variability in the selective environment are correlated, there will be a bias across the species towards environments experienced by the greatest number of individuals. Recently, adaptive evolution in species with a source-sink structure (e.g. at a species' border: Parsons, 1991; Hoffman and Blows, 1994) has been analysed (Holt and Gaines, 1992; Holt, 1996a). Typically (though not always) natural selection is biased toward the maintenance and improvement of adaptation in the source, at the expense of improved adaptation in the sink.

One general implication is that an ecological factor restricting a species' range may indirectly foster the evolution of habitat specialization, making the range restriction evolutionarily stable. For instance, in source-sink models, at moderate to low rates of dispersal, as the sink becomes a less fit habitat, the intensity of selection for improving fitness there weakens (Holt, 1996). The reason is that the force of selection is blindly biased towards those environments actually experienced by individuals in which individuals contribute relatively most toward future generations. Individuals in sinks have low fitness, and there tend to be few of them, so adaptation to the sink is 'devalued' by selection, relative to adaptation to the source.

It has been argued (Holt and Gaines, 1992; Holt, 1996) that this asymmetry in selection can explain phylogenetic conservatism in niche properties. A tendency towards niche conservatism may be greatly

enhanced if rare populations experience extinction, and are re-colonized from persistent, abundant populations (Harrison, 1991). Internal range dynamics can greatly influence a species' effective N_T. Whitlock (ms) shows that in metapopulations comprised of sources and sinks, effective N_e can be reduced far below census N_T. An understanding of the temporal dynamics of species' ranges is thus required to gauge the relative potential for long-term evolution in localized versus widespread species.

An important direction for future work will be to draw out the implications of spatial texture, spatial dynamics and range size for the rates of generation of evolutionary novelties, and speciation. Here are some closing thoughts.

- As noted above for within-community evolution, if the spatial texture of abundance is such that there are many more rare than common populations in a species' range, significant niche evolution within a lineage might be associated with rare populations, simply because there are more of them. However, this is not likely if most rare populations are sink populations, or experience rapid rates of extinction with re-colonization from more persistent, common populations (as in the island model above).
- Spatially restricted species may be more likely to evolve specific adaptations to local conditions (Futuyma, 1989). Such adaptations may be ephemeral in more widespread species, whose phenotypes express adaptive compromises to a heterogeneous, ever-shifting environment (Futuyma, 1989; Rosenzweig, 1995).
- Rosenzweig (1995) argues that the likelihood of allopatric speciation (number of daughter species per ancestral species) increases with range size, at least for small to medium ranges. There are two distinct effects here: the likelihood of isolate formation increases with range size, and large ranges may encompass a greater range of selective environments, permitting more divergent evolution among populations. This suggests that, as Darwin believed, 'common species' (= widespread species) should be the fount of speciation – even if speciation itself occurs most frequently in rare populations of those widespread species.
- Sexual species may have a cost of rarity, for instance because individuals must allocate more energy and time to finding mates. This cost may be most manifest in competitive interactions with less rare species, which do not incur such costs and thus can be more efficient resource exploiters. Hopf and Hopf (1985) and Michod (1995, Chapter 10) have argued that this effect of rarity may have important macroevolutionary consequences. Rare sexual species may be differentially vulnerable to competitive exclusion, leading to gaps in species' utilization functions along resource gradients. This mechanism works most forcefully when 'rarity' denotes low local population abundance, rather than range size. Community studies often reveal that habitat partitioning is far more

evident and fine-grained than local within-site resource partitioning among related taxa (Schoener, 1974). An intriguing possibility is that this generalization about community patterns may indirectly reflect the role of rarity in evolution.

We are just beginning to fathom the implications of spatial dynamics and spatial textures in abundance for evolution.

12.4 CONCLUSIONS

The problem of analysing the implications of rarity (viz., low population size and/or small range size) for evolution upon inspection has resolved into an interwoven tangle of problems. To reiterate this chapter's opening remarks, sensible questions about rarity and evolution require one to have a clear comparison in mind. Beyond this rather obvious (but often forgotten) point, the ruminations presented above are woven together by an emphasis on the importance of basic population dynamics. To reprise some of the main points:

- The effective population size of a species may differ greatly from its census size, because of long-term fluctuations in local abundance, range size, local extinctions and source-sink dynamics.
- The selective consequences of rarity cannot be evaluated without a crisp understanding of the dynamical reasons for rarity. Often, selection will not act in such a way as to make a rare species less rare; indeed, making a factor more important in limiting population size, or geographical range, may sometimes make it less important in selection. Ecological factors can affect population size with no effects on selection; little is known about how spatial variation in abundance reflecting ecological variation maps on to spatial variation in the selective environment.
- Considering the demographic effects of immigration into a sink reveals that the constraint on local adaptation may not quite be that gene flow hampers local selection (the conventional wisdom), but simply that the immigrants are maladapted to the local environment to start with. Ignoring the mechanisms of population dynamics can lead to a misunderstanding of the causal factors in evolutionary dynamics.

A clearer understanding of how population abundance and range size act as ecological drivers for evolutionary dynamics is particularly important for addressing many applied ecological problems. For instance, there is increasing focus on the genetics of rare populations, motivated by conservation concerns (e.g. Lande 1988; Falk and Holsinger, 1991; Schemske *et al.*, 1994). If population size scales the potential evolutionary response of species to changing environments, a species which has become rare because of environmental indignity A (e.g. habitat destruction) may thereby be unable to adapt to further environmental indignities X, Y and Z

(e.g. toxic wastes, pressure from invading exotics). As another example, the entire point of pest control programmes is to turn common species into rare species. For control to be anything other than a short-term palliative, evolutionary dynamics of the target pest must be considered. Evolutionarily stable pest control requires the imposition of strong limiting factors that do not evoke strong countervailing selection in the pest. Some of the most significant problems facing our species today thus lie squarely on the cusp between the ecological causes and evolutionary consequences of rarity.

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